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ORIGINAL ARTICLE

Another case of island gigantism: the extinct Hodgens' Waterhen (*Tribonyx hodgenorum*) is a member of *Porzana* (Aves: Rallidae)

George Sangster[1] · **Jacob C. Blokland**[2] · **Pascale Lubbe**[3] · **R. Paul Scofield**[4] · **Trevor H. Worthy**[2]

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Abstract

Tribonyx hodgenorum (Scarlett, Rec Canterb Mus 6:265–266, 1955) was a flightless rail (Rallidae) endemic to Aotearoa New Zealand that became extinct in the eighteenth century. The affinities of this rail have puzzled taxonomists, who have placed it in no less than six different genera. We present molecular phylogenetic evidence based on mitochondrial data that places *T. hodgenorum* within the *Porzana* clade as the sister taxon of Australian Crake (*P. fluminea*). This position was strongly supported but was not previously suspected. Thus, rather than a moderately small species of native-hen (*Tribonyx*), *T. hodgenorum* is a giant species of crake (*Porzana*). After the recent re-allocation of several species of '*Porzana*' to other genera, *P. hodgenorum* is the only known flightless species of *Porzana*. The genus name *Pyramida* Oliver, 1955, which is no longer in use, becomes a junior synonym of *Porzana* Vieillot, 1816. We suggest changing the English name of *P. hodgenorum* from Hodgens' Waterhen or New Zealand Native-hen to New Zealand Giant Crake.

Keywords Extinct birds · Flightlessness · Gigantism · Phylogeny · Taxonomy

Zusammenfassung

Ein weiterer Fall einer Riesenspezies: Das ausgestorbene Neuseeländische Pfuhlhuhn Tribonyx hodgenorum gehört zur Gattung Porzana (Aves: Rallidae).

Das Neuseeländische Pfuhlhuhn (Scarlett, Rec Canterb Mus 6:265–266, 1955) war ein flugunfähiger Vertreter der Rallen (Rallidae), der in Aotearoa (Neuseeland) endemisch war und im 18. Jahrhundert ausgerottet wurde. Die Verwandtschaftsverhältnisse dieser Ralle waren für die Taxonomen verwirrend, und sie haben sie derzeit nicht weniger als sechs verschiedenen Gattungen zugeordnet. Wir stellen hier einen molekularen, auf mitochondrialen Daten basierenden phylogenetischen Nachweis vor, der T. hodgenorum als ein Schwester-Taxon des Flusssumpfhuhns Porzana fluminea der Gattung Porzana zuordnet. Diese Zuordnung fand starke Unterstützung, war aber zuvor nicht wirklich erwartet worden. Somit ist T. hodgenorum keine verhältnismäßig kleine Art des einheimischen Huhns (Tribonyx), sondern eine Riesenspezies der Sumpfhühner (Porzana). Nachdem kürzlich mehrere „Porzana"-Arten anderen Gattungen zugeordnet wurden, ist P. hodgenorum nun die einzige bekannte flugunfähige Porzana. Der nicht mehr benutzte Gattungsname Pyramida Oliver, 1955, wird zu einem Untersynonym von Porzana Vieillot, 1816. Wir schlagen daher vor, den englischen Namen von P. hodgenorum von „Hodgens' Waterhen" oder „New Zealand Native-hen" in „New Zealand Giant Crake" zu ändern.

Introduction

Hodgens' Waterhen (also named New Zealand Native-hen or New Zealand Flightless Gallinule), most recently known in the combination *Tribonyx hodgenorum* (Scarlett 1955), was a flightless species of rallid (Rallidae) endemic to Aotearoa New Zealand. It is known from bones collected at multiple localities on the South Island (Scarlett 1955, 1970a,b; Worthy and Mildenhall 1989; Holdaway and Worthy 1997; Worthy 1997, 1998; Worthy and Holdaway 1996, 2002) and

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the North Island (Horn 1983; Worthy and Holdaway 2000), the most geologically recent of which derives from a midden that has been radiometrically dated to the eighteenth century (Cassels et al. 1988). On both North and South islands, nearly all sites where *T. hodgenorum* has been found derive from eastern regions, often in association with an Eastern fauna typified by *Chenonetta finschi* (Van Beneden 1876) and species of *Aptornis* Owen 1848, and none come from the many sites in closed canopy rimu-dominated rainforest or beech forest (e.g., Worthy 1997, 1998; Worthy and Holdaway 1996, 2000, 2002 [Figs. 14.6, and refs therein]). This indicates *T. hodgenorum* preferred swamps (e.g., Poukawa, Pyramid Valley) or grassland-shrubland mosaics of the seasonally dry eastern parts of Aotearoa New Zealand.

Tribonyx hodgenorum has an eventful taxonomic and nomenclatural history. It was described as *Rallus hodgeni* by Scarlett (1955) from Pyramid Valley Swamp, North Canterbury, South Island, though he acknowledged that its generic affinities were likely to change once more material could be attributed to it. The same year, Oliver (1955) recognised it had a close relationship to gallinules, specifically members of *Tribonyx* du Bus de Gisignies 1840, and placed the species in a new monotypic genus *Pyramida* Oliver 1955. This was followed by Scarlett (1969). Scarlett (1970a, b) subsequently placed *hodgeni* in the genus *Capellirallus* Falla 1954, overlooking the key features of the holotype pelvis mentioned by Oliver (1955) that supported gallinule affinities (e.g., the preacetabular ilia being largely unfused to the dorsal part of the synsacrum). Also at this time, Scarlett (1970a) described *Gallirallus hartreei* Scarlett 1970a from the cave Te Waka No. 1 in Hawkes Bay, and subsequently maintained that this was distinct from North Island occurrences of *hodgeni* that he listed under *Capellirallus hodgeni* North Island (see Scarlett 1970b). Comparisons, including newly recognised material of the skull and bill with those of the two extant Australian native-hens, *Tribonyx ventralis* (Gould 1837) and *T. mortierii* du Bus de Gisignies 1840, led Olson (1975) to transfer *hodgeni* to *Tribonyx*, which he considered a subgenus of *Gallinula* Brisson 1760. Olson (1975) further found that the species described as *Gallirallus hartreei* Scarlett 1970a, from the cave Te Waka No. 1, on the North Island, was not distinguishable from *Gallinula hodgeni*, and was synonymous with the latter species. Furthermore, Olson (1975) included most material that Scarlett (1970b) had listed as *Capellirallus hodgeni* North Island (some was recognised as misidentified *Capellirallus karamu* and/or *Gallirallus australis*) along with *Gallirallus hartreei* as *Gallinula (Tribonyx) hodgeni*.

This conclusion was subsequently challenged by Scarlett (1976), but Olson (1976) was not convinced and he listed *hartreei* under *Gallinula hodgeni* in his influential work on fossil rallids (Olson 1977). Olson (1986, 1987) emended the species name to *Gallinula hodgenorum* because Scarlett (1955) had named the species after two persons, although this was objected to by Mayr (1986). In Livezey's (1998) formal phylogenetic analysis of morphological characters, the species was recovered as part of a polytomy comprising *Tribonyx* (*T. ventralis, T. mortierii*), and species of *Pareudiastes* Hartlaub and Finsch 1871, *Edithornis* Mayr 1933, *Porphyriornis* Allen 1892, *Gallinula* and *Fulica* Linnaeus 1758. In view of the paraphyly of *Gallinula* (sensu Olson 1975), Livezey raised *Tribonyx* to full genus rank and listed Hodgens' Waterhen as *Tribonyx hodgenorum*. Since then, several molecular phylogenetic analyses (e.g., García-R et al. 2014a; Sangster et al. 2015; Boast et al. 2019; Kirchman et al. 2021) have robustly resolved the modern composition of the Fulicini Tribe, corroborated the paraphyly of *Gallinula* (sensu Olson 1975), and supported placement of *T. mortierii* and *T. ventralis* in *Tribonyx*. However, as no DNA sequences of *T. hodgenorum* were available, its placement in *Tribonyx* could not be confirmed. Nevertheless, following the placement of *hodgenorum* in *Tribonyx* (see Olson 1975; Livezey 1998), and the reinstatement of the name *Tribonyx* as a full genus based on both morphological and molecular phylogenetic evidence, *Tribonyx hodgenorum* has become the established name for the species (Gill et al. 2010; Checklist Committee OSNZ 2022).

The first DNA sequences of *T. hodgenorum* were two partial mitochondrial genomes, one from the North Island (GenBank accession number PQ723601) and another from the South Island (PQ723600; Lubbe et al. 2025). A phylogeny based on mitochondrial genomes found that *T. hodgenorum* was not sister to *Tribonyx ventralis* and diverged from the *Fulica* + *Gallinula* clade approximately 20 million years ago (Lubbe et al. 2025). However, the exact phylogenetic placement of *T. hodgenorum* in Fulicini could not be determined due to a lack of mitochondrial genomes of relevant taxa.

In this study, we use sequences from two mitochondrial markers to clarify the phylogenetic position of *T. hodgenorum*. We also justify its generic affinities using morphological character traits, address size evolution, and describe pertinent osteological differences between *T. hodgenorum* and its sister taxon.

Methods

We assessed the phylogenetic placement of *T. hodgenorum* with sequences of various species of Rallidae using two mitochondrial markers commonly used in avian phylogenetics. We used partial sequences of cytochrome oxidase subunit 1 (CO1, 696 bp) and the complete cytochrome b (CYB, 1143 bp) to infer phylogenetic relationships. Our data set included all three extant species of *Porzana* Vieillot 1816 (*P. porzana* (Linnaeus 1766), *P. carolina* (Linnaeus 1758), *P. fluminea* Gould 1843; for generic circumscription, see

Kirchman et al. 2021), all three species of *Tribonyx*, three species of *Gallinula*, *Paragallinula angulata* (Sundevall 1850), and up to ten species of *Fulica*. We also included sequences from several other rails (Table S1). *MUSCLE* (Edgar 2004; as implemented in MEGA7, Kumar et al. 2016) was used to align sequences. Maximum likelihood phylogenies were obtained using *IQ-tree* version 2.2.2.6 (Minh et al. 2020). We partitioned the data sets by codon. The appropriate substitution model for each partition in the two data sets was selected using *ModelFinder* (Kalyaanamoorthy et al. 2017). For CO1, the appropriate model for codon 1 and codon 2 was TIM2 + F + I + R3, and for codon 3, F81 + F + R2. For cytochrome b, the appropriate model for codon 1 and codon 2 was TVM + F + I + G4, and for codon 3, TIM2 + F + I + R2. Branch support was obtained using 1000 ultra-fast bootstraps (Hoang et al. 2018). We used sequences of *Sarothrura ayresi* (Gurney 1877) (GenBank accession number KY075897; du Plessis et al. 2017), *Heliornis fulica* (Boddaert 1783) (KF644581; García-R et al. 2014b) and *Nesotrochis steganinos* Olson 1974 (MW145005; Oswald et al. 2021) as outgroups based on their membership of the sister-clade of Rallidae in previous molecular studies (García-R et al. 2014a; Kirchman et al. 2021; Oswald et al. 2021). Details of all sequences used in the analyses are listed in electronic supplementary material Table S1.

Morphological comparisons were conducted using a light microscope, and measurements were made using a digital calliper accurate to 2 decimal places. Comparative material used include skeletal specimens from Canterbury Museum, Christchurch, New Zealand (CM), South Australian Museum, Adelaide, South Australia, Australia (SAMA), Museums Victoria, Melbourne, Victoria, Australia (NMV), Natural History Museum, Tring, United Kingdom (NHMUK), and Smithsonian National Museum of Natural History, Washington, United States of America (USNM), as follows: *Fulica americana* Gmelin 1789 (USNM 61074), *F. atra* (SAMA B36791, B58500, B39611, B39614, B49083, B39613, B37873), *F. cristata* Gmelin 1789 (USNM 558476), *Gallinula chloropus* (Linnaeus 1758) (SAMA B36875, USNM 603457), *G. tenebrosa* Gould 1846 (SAMA B31776, B37814, B47846), *Porphyriops melanops* (Vieillot 1819) (USNM 614595), *Porzana fluminea* (NMV B.11636, SAMA B10125, B31090, B31403, B32856, B34346, B45990, B46352, B48476, B49671, B5160), *P. carolina* (USNM 610786), *Tribonyx hodgenorum* (CM Av5854, Av5943, Av5985, Av6194, Av6196, Av6197, Av6646, Av7238, Av7338, Av8284, Av12906, Av15075, Av18475, Av20056, Av22951, Av43412, Av43413, Av43414, Av43415, Av43419, Av43420, Av43437, Av44009, Av45380, Av45381, Av45383, Av45384, Av48382, Av 2013.57.42), *T. mortierii* (NHMUK zoo:s/1970.4.3, SAMA B46032), and *T. ventralis* (CM Av 31,404, SAMA B31089, B38058, B39091, B46612, B47797, B48295, B48298, B48480, B48788, B49056, B49081, B49580, B56341, B58566). Published imagery, including fossil elements of *T. hodgenorum* such as those in Scarlett (1970a,b), Olson (1975, 1977), and Worthy and Holdaway (2002), were used in examining additional elements of this taxon. A skeletal specimen of *Paragallinula angulata*, the monotypic species of the only other genus in the tribe Fulicini, was not available for study. Considering the rapid evolution of flightlessness and its convergent effects on the pectoral skeleton especially, limited phylogenetic importance is placed on the forelimb elements, limiting intergeneric comparisons herein (see Olson 1973; Livezey 2003). As the holotype material of *Tribonyx hodgenorum* and *Gallirallus hartreei* are a partial pelvis (CM Av6197), and the associated hindlimb bones and humerus of an individual bird (CM Av18475), respectively, morphological comparisons are largely concentrated on these elements. Anatomical nomenclature follows Baumel et al. (1993), unless otherwise indicated. Taxonomic names follow the classification of Rallidae by Kirchman et al. (2021).

To verify Olson's (1975) statement, with regard to all North Island bones, that *"Gallirallus" hartreei* is "identical in size to *T. hodgeni*", we compared the measurements given in Olson (1975, Table 3) for *"Gallirallus" hartreei* (i.e., all bones of *hartreei* and those Scarlett 1970b called *Capellirallus hodgeni*) with our own measurements of *T. hodgenorum* from the South Island.

Results

Our phylogenetic analyses of Rallidae based on COI and cytochrome b place the two mitogenome sequences of *T. hodgenorum* among species in the genus *Porzana* with strong support (Fig. 1). A sister-group relationship between *T. hodgenorum* and *P. fluminea* was strongly supported in both gene trees. Uncorrected sequence divergence between *T. hodgenorum* from the South Island (PQ723600) and *Porzana fluminea* was 6.3% (COI) and 7.1% (cytochrome b).

Systematic Palaeontology

Rallidae Leach 1820

Fulicini Nitzsch 1820 (sensu Kirchman et al. 2021).

Porzana hodgenorum (Scarlett 1955).

Rallus hodgeni Scarlett 1955, p. 265

Pyramida [*hodgeni*] (Scarlett 1955); Oliver 1955, p. 595

Pyramidia hodgeni (Scarlett 1955); Oliver 1955, p. 596 (lapsus)

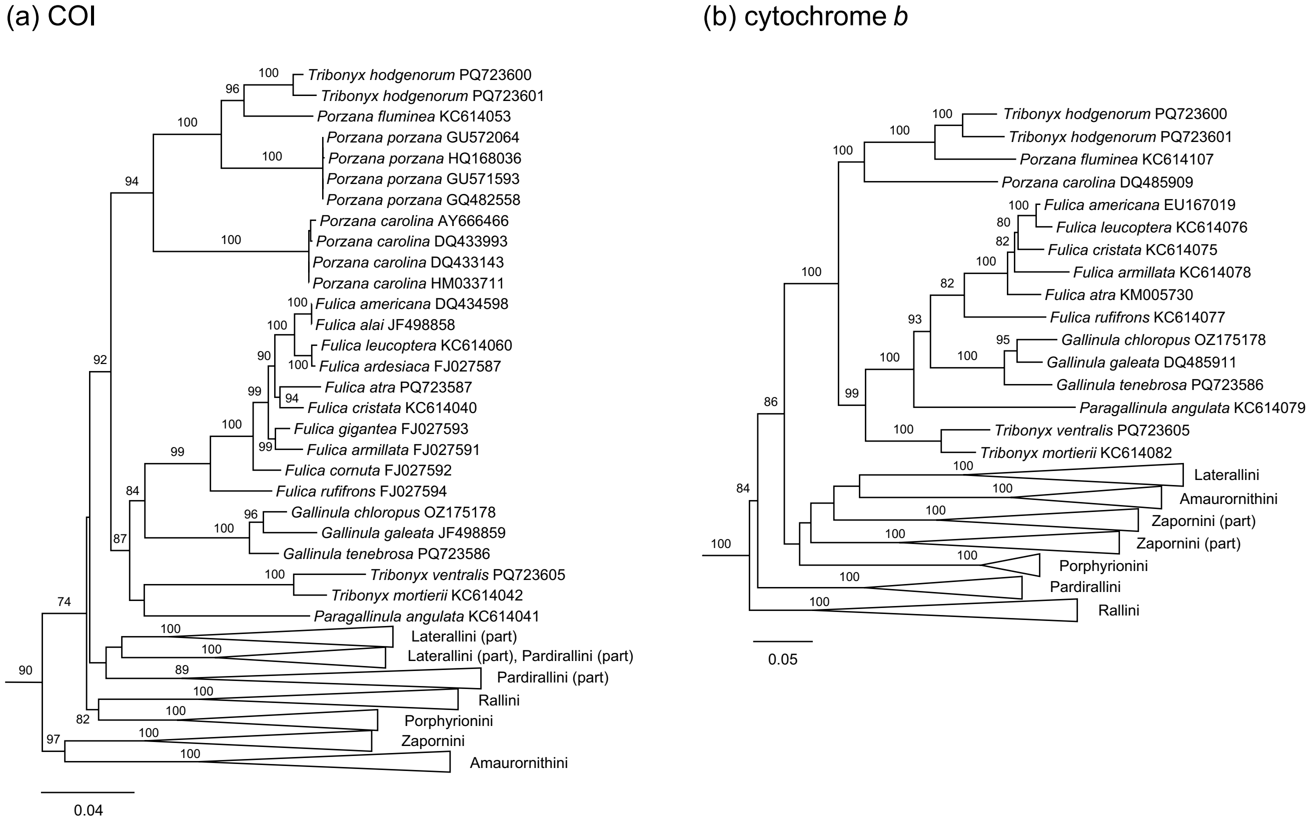


Fig. 1 Phylogenies of Rallidae based on mitochondrial genes showing the placement of *Tribonyx hodgenorum* among *Porzana*. The species label is followed by the relevant GenBank accession number. Several clades are collapsed and are denoted by higher taxon names as used in the classification of Kirchman et al. (2021). Outgroup taxa are not shown. Numbers along branches are bootstrap support values (> 70%)

Capellirallus hodgeni (Scarlett 1955); Scarlett 1970a, p.71, Scarlett 1970b, p. 304
Capellirallus lodgeni (Scarlett 1955); Scarlett 1970b, p. 306 (lapsus)
Gallirallus hodgeni (Scarlett 1955); Scarlett 1970a, p. 71 (lapsus)
Gallirallus hartreei Scarlett 1970a, p. 68
Pyramidula [*hodgeni*] (Scarlett 1955); Fleming (1975), p. 90 (lapsus)
Gallinula (*Tribonyx*) *hodgeni* (Scarlett 1955); Olson 1975, p. 68
Gallinula hodgeni (Scarlett 1955); Olson 1977, p. 370; Checklist Committee 1990, p. 123
Tribonyx hodgeni (Scarlett 1955); van Tets 1984, p. 472
Gallinula hodgenorum (Scarlett 1955); Olson 1986, p. 32 (emendation)
Tribonyx hodgenorum (Scarlett 1955); Livezey 1998, p. 2135
Porzana hodgenorum (Scarlett 1955); This paper (see discussion)

Especially notable osteological features that support the systematic affiliation of *T. hodgenorum* to Fulicini (sensu Kirchman et al. 2021) include a bill length from the base of the zona flexoria craniofacialis to the apex rostri maxillae that does not considerably exceed more than half of the rostrocaudal length of the entire skull. Additionally, *T. hodgenorum* shares with other species of Fulicini a pelvis that has the crista iliaca dorsalis of the ala praeacetabularis ilii both not consistently reaching the dorsal-most part of the crista spinosa synsacri and largely unfused to it, and also a preacetabular part of the ilium that is depressed along the midsection of its craniocaudal length (Fig. 2a–c; see Olson 1975, Fig. 6; Worthy and Holdaway 2002, Fig. 10.9). The latter character in particular has historically been used to ally *T. hodgenorum* with *Gallinula, Fulica* and *Tribonyx* (see Oliver 1955; Olson 1975), but also occurs in species of *Porphyriops* and *Porzana*.

Features in *T. hodgenorum* that are not shared with members of *Fulica* or *Gallinula* include a dorsoventrally deep upper jaw that is rostrocaudally short, bilaterally wide and triangular in cross-section from a rostral perspective. Olson

(1975) pointed to these characters in support of a close relationship to *Tribonyx* species. While the upper jaw of species in *Fulica* and *Gallinula* is short compared to most rallids, they are uniquely the most proportionally elongate and narrow within Fulicini; those of species within *Porphyriops, Tribonyx* and *Porzana* contribute to less than half of the rostrocaudal length of the skull, as in *T. hodgenorum*. From lateral perspective, the plane of the culmen and frontal region of the cranium are almost aligned in *T. hodgenorum*, a feature they share across species of the latter genera, but which differs strongly from the relatively more obtuse angulus craniofacialis of *Fulica* and *Gallinula* species.

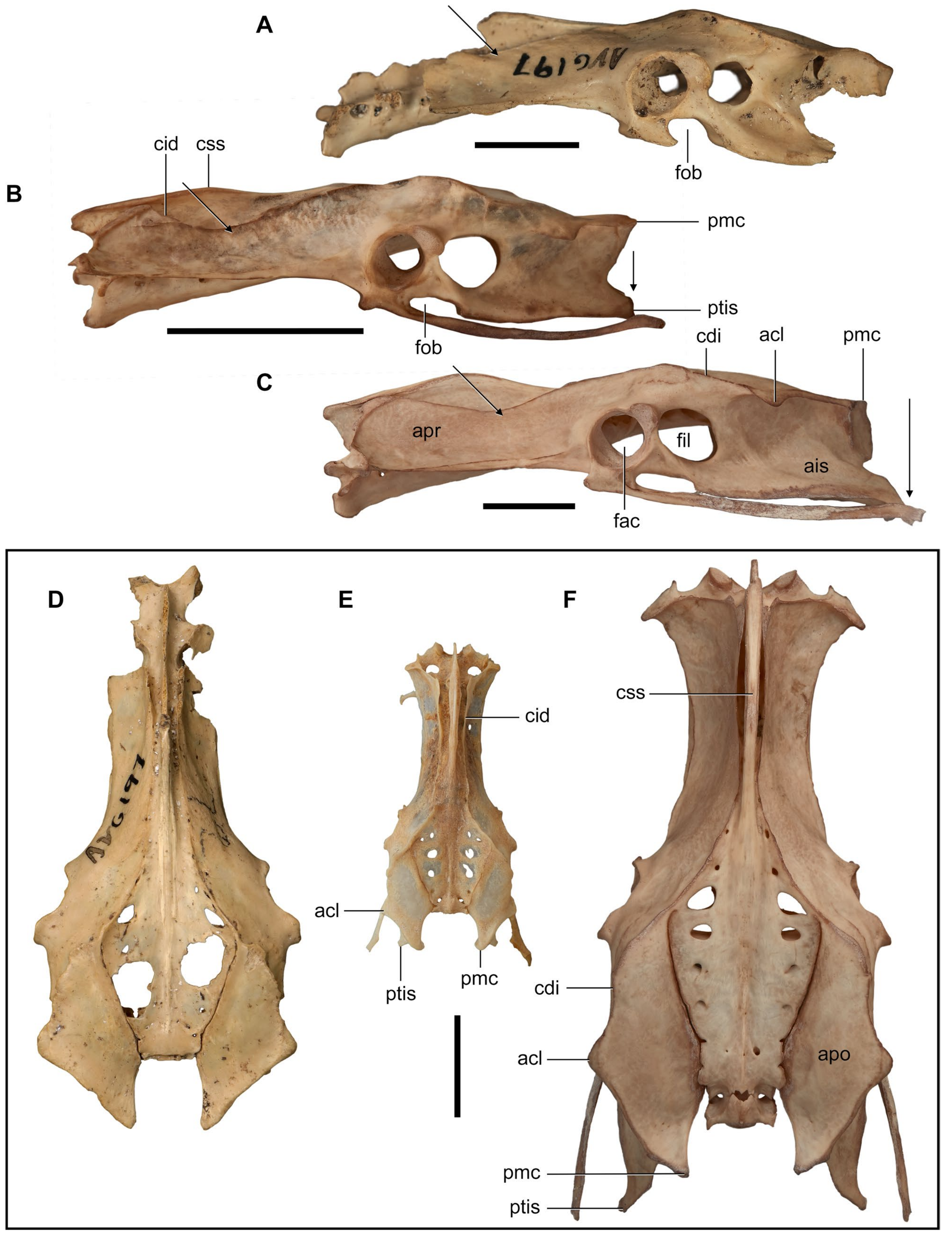
Oliver (1955) used characteristics of the pelvis to deduce that species of *Fulica* and *Gallinula* were not the closest relatives of *T. hodgenorum*. Compared to members of *Gallinula* and *Fulica*, the preacetabular and postacetabular regions of the pelvis of *T. hodgenorum* are bilaterally broader, the postacetabular ilium (processus marginalis caudalis, sensu Livezey and Zusi 2006) is less caudally developed, and the ala ischii is less laterally splayed. These differences in form are especially marked in comparison to the especially narrow and craniocaudally long pelvis of species in *Fulica*. Species of *Gallinula* further differ in that the crista iliaca dorsalis is more dorsally developed in the cranial region of the ala praeacetabularis ilii, for a greater part of the craniocaudal length of the preacetabular region of the pelvis. Close affinities with species of *Gallinula* and *Fulica* are thus clearly excluded on the basis of skull and pelvis morphology, and are not further alluded to in the comparisons below.

The angulus caudolateralis (sensu Livezey 1998; vertex caudolateralis ilii sensu Livezey and Zusi 2006) is a well-developed, laterally projected tab-like flange in *T. hodgenorum* and most members of Fulicini (Fig. 2), except *Porphyriops melanops* where it is craniocaudally broader. *Porphyriops melanops* further differs from *T. hodgenorum* and species of *Tribonyx* in its less dorsally elevated crista spinosa synsacri, and also from species of *Porzana* in an especially large foramen ilioischiadicum, and more caudally developed processus marginalis caudalis and less caudoventrally projected processus terminalis ischii. The latter structure is uniquely much more caudoventrally extended in both species of *Tribonyx* than in *T. hodgenorum*, species of *Porzana*, and all other members of Fulicini (Fig. 2b,c,e,f); Olson 1975, Fig. 6). *Tribonyx hodgenorum* and *Porzana fluminea* both have a preacetabular region that is relatively craniocaudally long, contributing more to the overall pelvis length than the postacetabular part, unlike species of *Tribonyx* where the preacetabular and postacetabular lengths are of similar proportions (Fig. 2a,b).

The femur of *T. hodgenorum* is similar to extant species of *Porzana* and differs from *Porphyriops melanops* and *T. ventralis* (but not *T. mortierii*, which is flightless), in that the lateral region of facies articularis antitrochanterica clearly proximally exceeds the proximal-most level of the caput femoris (Fig. 3d–f). Effectively, the femur caput is directed medially and encloses less of a notch proximally as do other taxa where the caput is directed more proximally. The femur of *T. hodgenorum* is similar to modern species of *Porzana* but differs from *Porphyriops melanops* and species of *Tribonyx*, in the presence of a proximodistally elongated depression that links the shaft to the fossa poplitea, laterad of linea intermuscularis caudalis on the distal quarter of the caudal femur; a more narrow sulcus patellaris and bounding medial and lateral crests; and contrasts with species of *Tribonyx* in that the crista tibiofibularis and semicondylus fibularis (sensu Elzanowski 2008) have proximal-most points that are nearly aligned, rather than being considerably distally offset as in the latter.

As in all species within Fulicini, on the tibiotarsus of *T. hodgenorum* the lateral part of the crista cnemialis cranialis is notably proximally displaced from the medial part, but not to the extreme degree observed in species of *Gallinula* and *Fulica*. Species of *Porzana, Porphyriops melanops*, and *T. hodgenorum* are distinguished from modern species of *Tribonyx* in having a non-angular and unpronounced proximal-most part of the crista fibularis; a distal opening of canalis extensorius that is mediolaterally wider than it is proximodistally tall; and a condylus lateralis that is only slightly cranially attenuated or expanded (Fig. 3g–i). *Tribonyx hodgenorum* differs from *Porphyriops melanops* in possessing a proportionally less mediolaterally extensive proximal opening of canalis extensorius (and pons supratendineus), and lacking a developed, flange-like proximal apex of the crista trochlearis medialis (sensu Kuročkin et al. 2015). It is united with species of *Porzana* in that the incisura intercondylaris is narrowed by the lateral (internal) side of condylus medialis slightly overlapping in alignment with the distal opening of canalis extensorius, and a low, poorly developed tuberculum associated with the attachment of ligamentum meniscotibiale (lateral of pons supratendineus on condylus lateralis; Fig. 3g, h).

All rallids in Fulicini have an enclosed canal for the passage of flexor digitorum longus on the medial side of the hypotarsus (albeit variably enclosed or open in specimens of *T. mortierii*, also see Mayr 2019 regarding the structure of the hypotarsus in rails), and *T. hodgenorum* is no exception. A noticeably swollen proximodorsal edge of the tarsometatarsus, distad to cotyla medialis, is frequently observed in members of this tribe, and this has been highlighted as characteristic of *T. hodgenorum* ("*protuberance on the inner side of the shaft*", with reference to *Gallirallus hartreei*, see Scarlett 1970a; Fig. 3j–l). The derived, proportionally proximodistally shorter and robust tarsometatarsus of *T. hodgenorum* starkly contrasts with the more-slender form of *Porphyriops melanops* and the especially gracile proportions of rails in *Porzana* and *Tribonyx* (a maximum proximodistal length to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◂**Fig. 2** Comparisons of pelves of the flightless New Zealand Giant Crake and related volant species. Pelves are displayed in left lateral aspect, resized to facilitate comparison of osteology (A–C), and in dorsal aspect at the same scale (D–F). *Tribonyx hodgenorum* in A and D (CM Av 6197, holotype); *Porzana fluminea* in B (SAMA B34346) and E (NMV B.11636); *Tribonyx ventralis* in C and F (SAMA B48480). Abbreviations: acl, angulus caudolateralis; ais, ala ischii; apo, ala postacetabularis ilii; apr, ala praeacetabularis ilii; cdi, crista dorsolateralis ilii; cid, crista iliaca dorsalis; css, crista spinosa synsacri; fac, foramen acetabuli; fil, foramen ilioischiadicum; fob, foramen obturatum; pmc, processus marginalis caudalis; ptis, processus terminalis ischii. Arrows at 45° indicate the depressed area of ala praeacetabularis ilii, while vertical arrows show the comparative caudoventral extent of processus terminalis ischii. All scale bars are equal to 10 mm

minimum mediolateral shaft width ratio of approximately 10.7 in *T. hodgenorum* compared to around 16 in species of *Porzana* and *Tribonyx*; Fig. 3j–l, also see Table 1).

There are few especially noticeable similarities in tarsometatarsus morphology that unambiguously unite *T. hodgenorum* to one genus within Fulicini. It differs from *Porphyriops melanops* in the lack of a dorsoplantarly narrow width of the medial shaft margin (between crista plantaris medialis and facies dorsalis), and the shallower, less medial torsion of the proximal sulcus extensorius and the shaft (corpus tarsometatarsi). At the distal end, the proximal surface of the dorsal trochlea metatarsi IV proximally exceeds that of trochlea metatarsi III in *T. hodgenorum*, *Porphyriops melanops* and species of *Porzana*, but is proximodistally aligned in species of *Tribonyx*. Its tarsometatarsi are similar to members of *Porzana*, to the exclusion of *Porphyriops melanops* and species of *Tribonyx* in that the lateral edge of the dorsal trochlea metatarsi III conspicuously bulges laterally, and from only *Porphyriops melanops* by the distal-most side of the dorsal opening for foramen vasculare distale and canalis interosseus distalis being clearly proximally displaced from alignment with the proximal-most part of trochlea metatarsi III (Fig. 3j–l).

Comparisons of the measurements given in Olson (1975, Table 3) for North Island *T. hodgenorum* (i.e., all bones of *hartreei* and those Scarlett 1970b called *Capellirallus hodgeni*) with our own measurements of *T. hodgenorum* from the South Island showed that North Island birds were significantly larger in size in all characters (two-tailed *t*-test, Table 1).

Discussion

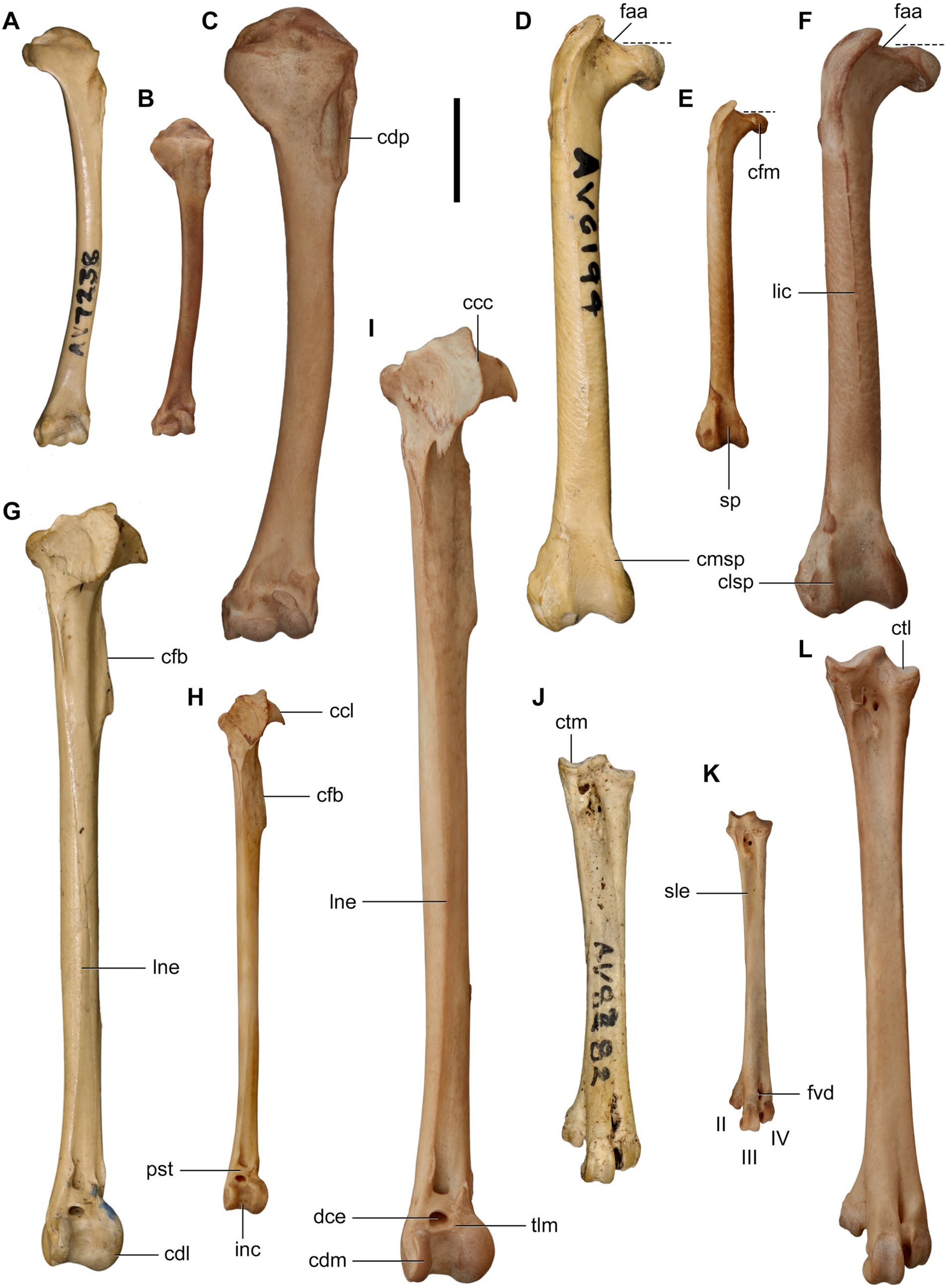
Phylogenetic placement

Our phylogenetic analyses of two mitochondrial markers show that *T. hodgenorum* is not closely related to the two extant species of native-hen *Tribonyx* (*T. ventralis*, *T. mortierii*). Instead, *T. hodgenorum* is part of the *Porzana* clade with strong support in both the COI gene tree and the cytochrome b gene tree. This relationship is also corroborated through morphological features of the skull, pelvis and hindlimb skeleton. Our findings show that *T. hodgenorum* should be placed in the genus *Porzana* to become *P. hodgenorum. Porzana* was hitherto only known in New Zealand from a single vagrant *P. fluminea* (Checklist Committee OSNZ 2022). Due to the removal of *P. hodgenorum*, the genus *Tribonyx* (type species *T. mortierii*) should be restricted to two extant species, *T. mortierii* and *T. ventralis*. A third taxon, the extinct *Tribonyx mortierii repertus* (de Vis 1888), is currently treated as a subspecies of *T. mortierii* (see Olson 1975, 1977; Worthy and Nguyen 2020). The genus name *Pyramida* Oliver 1955, which is no longer in use, becomes a junior synonym of *Porzana.*

Flightlessness in *Porzana*

Until recently, the genus *Porzana* included multiple flightless species. Following clarification of relationships through the use of molecular data, all flightless species were placed in other genera (*Zapornia* Leach 1816, *Laterallus* Gray 1855, *Hapalocrex* Ridgway 1920). Four extant or historically known flightless species, *Z. atra* (North 1908), *Z. monasa* (Kittlitz 1858), *Z. palmeri* (Frohawk 1892), *Z. sandwichensis* (Gmelin, JF, 1789), are now included in *Zapornia* (see Dickinson and Remsen 2013; Gill et al. 2024) based on molecular data (Slikas et al. 2002). Two other flightless species from Hawaii, *'Porzana' keplerorum* Olson and James 1991, and *'Porzana' severnsi* Olson and James 1991, were originally described in the genus *Porzana* but phylogenetic analysis of morphological characters of Livezey (1998) constrained by molecular data of extant species reconstructed these as members of the *Zapornia* clade (García-R and Matzke 2021). In the same study, the flightless *'Porzana' astrictocarpus* Olson 1973, of Saint Helena, and *'Porzana' menehune* Olson and James 1991 of Molokai, Hawaiian Islands, were placed in a clade with members of the genus *Laterallus*, and another two flightless Hawaiian species, *'Porzana' ralphorum* Olson and James 1991 and *'Porzana' ziegleri* Olson and James 1991, were reconstructed as members of a clade of '*Gallirallus*' de Lafresnaye 1841 rails (=*Hypotaenidia* Reichenbach 1853, sensu Kirchman et al. 2021) within the tribe Rallini (see Garcia-R and Matzke 2021).

Species of *Laterallus* are known to inhabit the Americas and nearby islands (e.g., Galápagos Islands, see Taylor 1998), although their range extends to the remote South Atlantic Ocean (e.g., *Laterallus rogersi*, Inaccessible Island, Stervander et al. 2019), and so may be expected to occur on Saint Helena. However, crakes within the genus *Zapornia* are relatively widespread across the Pacific in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◂**Fig. 3** Comparisons of the humerus and major hind limb bones of the flightless New Zealand Giant Crake and related volant species, to scale. Left humeri in cranial aspect (**A**–**C**), right femora in cranial aspect (**D**–**F**), left tibiotarsi in cranial aspect (**G**–**I**) and left tarsometatarsi in dorsal aspect (**J**–**L**). *Tribonyx hodgenorum* in A (CM Av 7338), D (CM Av 6194), G (CM Av 5854) and J (CM Av 8282); *Porzana fluminea* in **B**, **E**, **H** and **K** (SAMA B34346); *Tribonyx ventralis* in **C**, **F**, **I** and **L** (SAMA B48480). Abbreviations: *ccc* crista cnemialis cranialis, *ccl* crista cnemialis lateralis, *cdl* condylus lateralis, *cdm* condylus medialis, *cdp* crista deltopectoralis, *cfb* crista fibularis, *cfm* caput femoris, *clsp* crista lateralis sulci patellaris, *cmsp* crista medialis sulci patellaris, *ctl* cotyla lateralis, *ctm* cotyla medialis, *dce* distal opening of canalis extensorius, *faa* facies articularis antitrochanterica, *fvd*, foramen vasculare distale; *II* trochlea metatarsi II, *III* trochlea metatarsi III, *IV*, trochlea metatarsi IV, *inc* incisura intercondylaris, *lic* linea intermuscularis cranialis, *lne* linea extensoria, *sle* sulcus extensorius, *sp* sulcus patellaris, *tlm* tuberculum associated with the attachment of ligamentum meniscotibiale. Dashed lines in **D**–**F** align with the proximal-most level of the caput femoris (see text). Note that parallax may distort and affect the alignment of structures at extremities. Scale bar is equal to 10 mm

both historic and modern times, and are known from the Hawaiian Islands. Species of *Laterallus* and *Gallirallus* are unreported from these islands (Steadman 2006; Worthy et al. 2025), suggesting affiliation to *Zapornia* may be more likely for most of these Hawaiian taxa (or perhaps *Porzana* given the rare vagrancy of *P. carolina*, e.g., Uyehara 2004). Considering the inconsistencies between morphology-based phylogenetic relationships of crakes resolved by Livezey (1998) and those derived from genetic data (e.g., Slikas et al. 2002; Boast et al. 2019; Kirchman et al. 2021), robust taxonomic assignment of these Hawaiian fossil taxa awaits more detailed osteological analysis and the use of molecular information.

'Porzana' rua Steadman 1986, from the Cook Islands, was flightless (Steadman 2006) and found in sympatry with *Zapornia tabuensis*, but whether it was an earlier arrival of this lineage has not been determined. Finally, the flightless *'Porzana' piercei* Olson and Wingate 2000, from Bermuda, was characterized in the original description as very similar to the extant '*P*'. *flaviventer* (Boddaert 1783) (now *Hapalocrex flaviventer*; see Kirchman et al. 2021), and likely also represents a member of the genus *Hapalocrex*. The genus *Porzana* therefore currently consists of three extant species, *P. carolina*, *P. porzana* and *P. fluminea*, and two extinct species, *P. botunensis* Boev 2015 and *P. hodgenorum*. Thus, based on present evidence, *P. hodgenorum* is the only known species of *Porzana* that was flightless.

Size and weight

New Zealand avian speciation is frequently associated with an increase in size and weight, a complete loss or reduction of flight capacity and changes in proportional leg length commensurate with behavioural changes (Worthy and Holdaway 2002). Livezey (2003) counted "*Tribonyx*" *hodgenorum* as a notable exception to the general association between increased body mass and the evolutionary loss of flight in rails, and among the minority of flightless rallids that can be considered insular dwarfs (e.g., *Hypotaenidia modesta* [Hutton 1872], *H. wakensis* Rothschild 1903, *Laterallus rogersi* [Lowe 1923]). With an estimated body mass of 313 g in males and 263 g in females (Livezey 2003), this species is indeed smaller than *T. ventralis* (410 g in males, 364 g in females; Marchant and Higgins 1993) and remarkably so in comparison with the flightless *T. mortierii* (1334 g in males, 1251 g in females; Marchant and Higgins 1993). However, the placement of *P. hodgenorum* in *Porzana* switches the direction of size change in *P. hodgenorum* to gigantism, as its Australian sister-species *P. fluminea* (66 g in males, 57 g in females; Marchant and Higgins 1993) and two other close relatives (*P. porzana*, 87 g; *P. carolina*, 75 g; Dunning 2008) are no less than three to six times smaller.

Leg length

A disproportionate increase in leg length relative to weight has been argued as indicative of a propensity to spend a greater amount of time on the ground (Worthy and Holdaway 2002; Livezey 2003). New Zealand taxa that exhibit this change include *Ninox* Hodgson 1837*, Fulica,* and *Petroica* Swainson 1829. Surprisingly, despite a three- to six-fold increase in weight compared to its sister taxon *P. fluminea*, the tarsometatarsus length of *P. hodgenorum* increased by only one third. This relatively short tarsometatarsus is a characteristic seen in other New Zealand flightless rails (Livezey 2003, Table 33): the weka, *Gallirallus australis* (Sparrman 1786), has a relatively shorter tarsometatarsus (femur:tarsometatarsus ratio 1.18) than that of *Hypotaenidia philippensis* (1.12), which is often taken to represent the bauplan of the ancestral flightless oceanic *Gallirallus*-like rails (e.g., Mayr and Diamond 2001; Livezey 2003; Kirchman 2009, 2012). On this trend, *Diaphorapteryx hawkinsi* (Forbes 1892a) has an even shorter tarsometatarsus (femur:tarsometatarsus ratio 1.34). *Porzana hodgenorum*, with a femur:tarsometatarsus ratio of 1.36, therefore has similar proportions to *Diaphorapteryx* Forbes 1892b. In larger flightless birds, such as those observed in species of *Aptornis* a proportional decrease in tarsometatarsus length is interpreted as a shift towards graviportality, contributing to a broader and more stable foot (Storer 1971). It is difficult to understand the evolutionary advantage of short tarsometatarsi in *P. hodgenorum*, but Andrews (1896) suggested such proportions may have been related to using the feet to forage, as is often observed in modern *Gallirallus australis* scratching through soil or leaf litter. This adaptation may suggest

Table 1 Measurements (mm) and comparison of hindlimb bone lengths of selected species of Fulicini and *Tribonyx hodgenorum*, and their proportional contribution to Total leg length is derived from the sum of the proximodistal lengths of the femur, tibiotarsus (art) (measured proximally from the surface for articulation with the femur), and tarsometatarsus, excluding phalanges

TAXON	Femur			Tibiotarsus (cnem)			Tibiotarsus (art)			Tarsometatarsus			Leg length	Proportion of limb length		
	L	s.d	*n*	L	s.d	*n*	L	s.d	*n*	L	s.d	*n*		Fem	Tib	Tmt
Fulica atra	52.63	1.96	7	94.91	5.15	7	89.85	5.15	7	54.79	3.24	7	197.28	26.7	45.5	27.8
Gallinula chloropus	50.27	4.69	2	81.65	7.36	2	78.41	6.52	2	52.33	5.57	2	181.00	27.8	43.3	28.9
Gallinula tenebrosa	60.81	1.58	4	100.35	3.95	4	96.28	4.24	4	61.03	3.13	4	218.12	27.9	44.1	28.0
Porphyriops melanops	41.77	–	1	68.52	–	1	65.72	–	1	41.55	–	1	149.04	28.0	44.1	27.9
Porzana fluminea	32.00	1.03	10	48.94	1.45	8	47.14	1.35	8	29.94	0.97	10	109.08	29.3	43.2	27.4
Tribonyx mortierii	82.26	0.86	2	133.82	4.54	2	128.99	5.18	2	81.22	1.98	2	292.46	28.1	44.1	27.8
Tribonyx ventralis	56.11	2.82	14	93.71	5.21	13	90.41	4.78	13	60.77	3.04	14	207.30	27.1	43.6	29.3
Tribonyx h. hodgenorum	55.78	1.73	25	74.16	2.31	20	72.05	2.00	21	41.22	1.29	12	169.20	33.0	42.7	24.3
Tribonyx h. hartreei	58.40	2.39	45	76.00	1.66	19	74.00	1.59	25	43.00	2.10	46	175.40	33.3	42.2	24.5
t-test Significance	> .0001			> .0001			> .0001			> .0001						

Where specimens corresponding to a known individual had both left and right bones available in appropriate condition to measure, an average length was derived ($n = 1$). *t*-test significance compares North and South Island *Tribonyx hodgenorum* specimens only

Abbreviations: *art* measured from the proximal-most surface for articulation with the femur, *cnem* measured from the proximal-most crista cnemialis cranialis (i.e., maximum tibiotarsus length), *fem* femur, *L* proximodistal length, *n* number of specimens measured, *s.d.* standard deviation, *tib* tibiotarsus, *tmt* tarsometatarsus

that *P. hodgenorum* was less well-adapted for high-speed terrestrial locomotion.

Morphology: qualitative species differences

Morphological studies comparing *P. hodgenorum* with other rallids have largely neglected comparison with species of *Porzana* (see Scarlett 1955, 1970a,b; Olson 1975, 1977). Scarlett (1970b) noted that the shallow keel of the sternum of *P. hodgenorum* differed from those of species of "*Porzana*", although it is not known whether the taxa used were members of this genus as it is currently understood (i.e., sensu Kirchman et al. 2021). Livezey (1998) compared members of *Porzana* with *P. hodgenorum* through phylogenetic analysis of morphological characters, but did not resolve a close relationship between these taxa, nor did he recover other relationships now supported by molecular data (Kirchman et al. 2021). Given the sister relationship indicated by molecular analyses presented here, it is worth documenting morphological differences between *P. hodgenorum* and *P. fluminea* to affirm the species status of *P. hodgenorum*.

Livezey (1998) recorded nine osteological differences between *T. hodgenorum* and *P. fluminea* in his character matrix of 570 anatomical characters. Of these characters, we have been able to corroborate only six. We were able to verify that *T. hodgenorum* differed from *P. fluminea* in that the processus jugalis of os maxillare (for arcus jugalis) is distinctly dorsally displaced from the tomial margin of the maxilla (ch. 31); the dorsal surface of the ossa frontalia is not depressed (lacks depressio frontalis, ch. 70); the fossa temporalis is better defined (ch. 80); the cranial part of the sternum has a poorly developed medial strut on its dorsal surface for supporting the coracoid articulation (ch. 139); the spina externa rostri is absent (ch. 163); and that the caudolateral profile of the ala postacetabularis ilii in dorsal perspective is nearly linear in *T. hodgenorum* but concave in *P. fluminea* (see char. 287, coded oppositely by Livezey 1998).

In contrast to the morphological states coded in Livezey's study, it is instead observed that the pelvis of both species has a foramen ilioischiadicum that is most elongate in the craniodorsal-caudoventral direction (albeit approximating a more circular shape in some specimens of *Porzana fluminea*, ch. 261), and that the dorsal-most part of crista iliaca dorsalis does not unite with the dorsal-most part of crista spinosa synsacri across the craniocaudal length of the preacetabular ilia in either taxon (ch. 275). Both taxa also have a closed canal on the medial side of the hypotarsus of the tarsometatarsus for the passage of flexor digitorum longus (ch. 337), in contrast to Livezey's (1998) coding that this passage is a plantarly open sulcus in *P. fluminea*.

The most noticeable difference between *P. hodgenorum* and its sister taxon, *P. fluminea*, is its much greater size and estimated mass, in relation to relative insular gigantism following the loss of flight (see above). The evolution of flightlessness has also predictably manifested several major changes in the skeleton of in *P. hodgenorum* which differ from the volant *P. fluminea*, especially with regards to its vestigial pectoral apparatus, and associated proportionally proximodistally shortened and intraspecifically variable forelimb element morphologies (see Olson 1973, 1975, 1977; Livezey 1998, 2003). Olson (1975, 1977) remarked on several of these when comparing modern flighted and flightless *Tribonyx* species, and numerous flightlessness-related apomorphies of the sternum, furcula, scapula, coracoid, and the wing skeleton (ossa alae) possessed by *P. hodgenorum* were extensively listed by Livezey (2003, tables 58–61, 63–64). In association with the loss of flight, *P. hodgenorum* has a comparably hyperdeveloped pelvic girdle and hindlimbs that are relatively specialised for terrestrial locomotion. In addition to general exaggeration and hypertrophy of muscle and ligament attachment areas on these bones, the pelvis of *P. hodgenorum* has a more dorsally elevated crista spinosa synsacri in the preacetabular region, and more splayed, robust trochlea of the tarsometatarsi. It is also characterised by conspicuously different leg proportions, consisting of a more elongated femur, and a shortened, stocky tarsometatarsus that contributes less to the total leg length (Table 1; Storer 1971; Livezey 2003); see 'leg length'. The skull of *P. hodgenorum,* which has a more dorsoventrally deepened upper jaw than that of *P. fluminea*, and a more dorsally arched culmen, are likely specialisations indirectly associated with loss of flight, reflective of foraging differences driven by insular environmental and ecological conditions and more sedentary lifestyle (Livezey 2003; Gussekloo and Cubo 2013).

The taxonomic status of *Gallirallus hartreei* Scarlett 1970a

Previously published and our own measurements show that bones of *T. hodgenorum* from the North Island (incl. "*G.*" *hartreei*) are significantly larger than those from the South Island. This contradicts Olson's (1975) statement that *"Gallirallus" hartreei* is "identical in size to *T. hodgeni*". Given these size differences (which counter Bergmann's Rule) and the recently reported molecular differences between North and South Islands (Lubbe et al. 2025), the North Island population is here tentatively treated as a subspecies, *Porzana hodgenorum hartreei*. However, we note the North and South Island populations lack skeletal proportional differences and think assessment of species-level status will require a full analysis of morphology and more detailed molecular analyses.

English name

Porzana hodgenorum was previously named 'Hodgens' Waterhen' (Holdaway and Worthy 1997; Gill et al. 2010; Checklist Committee OSNZ 2022; Lubbe et al. 2025). This name was coined when the species was still classified as a member of *Gallinula*. The name 'New Zealand Native-hen' has also been used for this species and reflects its placement in *Tribonyx* at the time (Livezey 1998). A third name given to this species is New Zealand Flightless Gallinule (Hume 2017). To reflect its phylogenetic position among *Porzana* crakes and its large size compared with its sister-taxon *P. fluminea*, we suggest that *P. hodgenorum* is appropriately called 'New Zealand Giant Crake'.

The spelling of the name *hodgenorum*

The species was described as *Rallus hodgeni* by Scarlett (1955), who named it "after Messrs J. and R. Hodgen, owners of Pyramid Valley swamp". Olson (1986) emended this name to *hodgenorum*, because the name was given to two persons both named Hodgen. This spelling is now universally adopted (e.g., Livezey 1998, 2003; Worthy and Holdaway 2002; Gill et al. 2010; Hume 2017; Checklist Committee OSNZ 2022).

Olson (1986) regarded *hodgeni*, in the combination *Rallus hodgeni*, as an incorrect original spelling, following Art. 31c of ICZN (1985). Article 31c of that version of the Code deals with the appropriate endings for Latin or Latinized adjectival and participial names and refers to Appendix D for instructions on how such names should be written. Article 32c(ii) states that "[a]n original spelling is an 'incorrect original spelling' if there is in the original publication itself, without re-course to any external source of information, clear evidence of an inadvertent error, such as a lapsus calami or a copyist's or printer's error (incorrect transliteration or latinization and use of an inappropriate connecting vowel are not to be considered inadvertent errors)" (ICZN 1985, 69). This was followed by an example that is nearly identical to that of *Rallus hodgeni*: "*douglasi*, in *Eptesicus douglasi*, said to be named after Marion and Athol Douglas, is an incorrect original spelling that must be corrected to *douglasorum*" (ICZN 1985, 69). This example demonstrates that Olson (1985) was justified in (i) considering the name *hodgeni* as an incorrect original spelling and (ii) emending the name to *hodgenorum*.

However, Article 32.5 in the most recent version of the Code (ICZN 1999) includes an almost identical rule but excludes the aforementioned example. This makes interpretation of the correct spelling of the name *hodgenorum* more complicated. Article 31.1.2 (ICZN 1999) states that a species-group name, if a noun in the genitive case formed directly from a modern personal name, is to be formed by adding to the stem of that name -*orum* if the personal name is that of men. However, this instruction should not be retroactively applied to existing names that are believed to be incorrect, such as *hodgeni*. Article 31.1.3 indeed states that ‘The original spelling under Art. 31.1.1 and 31.1.2 is to be preserved [Art. 32.2] unless it is incorrect [Arts. 32.3, 32.4]’. Article 32.4 (ICZN 1999) states that an original spelling is an "incorrect original spelling" if it must be corrected as required in Article 32.5. The conditions for spellings that must be corrected (Art. 32.5) do not explicitly include the use of incorrect terminations to a noun formed from a modern personal name, nor do they explicitly exclude these. In any case, as noted above, Art. 32.5 (ICZN 1999) is nearly identical to Art. 32c(ii) in the 1985 version, under which *hodgeni* was clearly to be regarded as an incorrect original spelling. Taken at face value, under Art. 33.1 and Art. 33.4 (ICZN 1999), Olson (1986) made an incorrect subsequent spelling (as defined by Art. 31.1, ICZN 1999), because an emendation (Art. 33.2) is excluded under Art. 33.4. This being so, Art. 33.3 (ICZN 1999) has ascendency, and so *Gallinula hodgenorum* Olson 1986 would not be an available name (and not a synonym). However, because Olson (1986) attributed the species epithet *hodgenorum* to Scarlett (1955), and the spelling *hodgenorum* is in prevailing usage, the subsequent spelling and attribution are to be preserved and the spelling *hodgenorum* is deemed to be a correct original spelling (Art. 33.3.1).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10336-025-02316-x.

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Data availability The morphological datasets generated during and/or analysed during the current study are not publicly available but are available from the corresponding author on reasonable request. The DNA sequences can be accessed from GenBank (https://www.ncbi.nlm.nih.gov/nucleotide) using the accession numbers listed in Fig. 1a and 1b.

Declarations

Conflict of interest The authors declare that there are no conflicts of interest.

References

Allen JA (1892) Description of a new gallinule from Gough Island. Bull Am Mus Nat Hist 4:57–58

Andrews CW (1896) Note on the skeleton of *Diaphorapteryx hawkinsi*, Forbes, a large extinct rail from the Chatham Islands. Geol Mag 3:336–338

Baumel JJ, King AS, Breazile JE, Evans HE, Vanden Berge JC (1993) Handbook of avian anatomy. Nomina Anatomica Avium, 2nd Edition. Publication No. 23, Publications of the Nutall Ornithology Club, Cambridge, Massachusetts

Boast AP, Chapman B, Herrera MB, Worthy TH, Scofield RP, Tennyson AJD, Houde P, Bunce M, Cooper A, Mitchell KJ (2019) Mitochondrial genomes from New Zealand’s extinct adzebills (Aves: Aptornithidae: *Aptornis*) support a sister-taxon relationship with the afro-Madagascan Sarothruridae. Diversity 11:24

Boddaert P (1783) Table des planches enluminéez d’histoire naturelle de M. D’Aubenton. Utrecht

Boev ZN (2015) *Porzana botunensis* sp. n., a new Early Pleistocene crake (Aves: Rallidae) from Bulgaria. Acta Zool Bulg 67:283–290

Brisson MJ (1760) Ornithologie, ou, Méthode Contenant la Division des Oiseaux en Ordres, Sections, Genres, Especes & leurs Variétés. Volume 1. Jean-Baptiste Bauche, Paris

Cassels RJS, Jones KL, Walton A, Worthy TH (1988) Late prehistoric subsistence practices at Parewanui, Lower Rangitikei River, New Zealand. New Zealand J Archaeol 10:109–128

Checklist Committee (EG Turbott, Convener) (1990) Checklist of the birds of New Zealand and the Ross Dependency, Antarctica (3rd edition). Ornithological Society of New Zealand & Random Century New Zealand Ltd. Xvi, Auckland

Checklist Committee OSNZ (2022) Checklist of the Birds of New Zealand (5th edition). Ornithological Society of New Zealand Occasional Publication No. 1. Ornithological Society of New Zealand, Wellington

de Lafresnaye NFAA (1841) Nouvelles espèces d’oiseaux décrites. Rev Zool Soc Cuvier 1841:241–243

de Vis CW (1888) A glimpse of the post-Tertiary avifauna of Queensland. Proc Linn Soc N S Wales 3:1276–1292 + pl. XXXIII–XXXVI

Dickinson EC, Remsen JV (2013) The Howard and Moore complete checklist of the birds of the world. Fourth edition, vol. 1: Non-passerines. Aves Press, London

du Bus de Gisignies B (1840) Description d’un nouveau genre d’oiseau de la famille des Gallinules. Bull Acad R Sci Bell-Lettr Bruxelles 7:212–215

du Plessis M, Dalton DL, Smit-Robinson HA, Kotze A (2017) Next generation sequencing yields the mitochondrial genome of the critically endangered *Sarothrura ayresi* (White-winged Flufftail). Mitochondrial DNA Part B 2:236–237

Dunning JJB (2008) CRC handbook of avian body masses, 2nd edn. CRC Press, Boca Raton, FL

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucl Acids Res 32:1792–1797

Elzanowski A (2008) The avian femur: morphology and terminology of the lateral condyle. Oryctos 7:1–5

Falla RA (1954) A new rail from cave deposits in the North Island of New Zealand. Rec Auckl Inst Mus 4:241–244

Fleming CA (1975) “A Classification of the Rallidae” by Storrs L. Olson [Review]. Notornis 22:90–91

Forbes HO (1892a) New extinct rail (telegram). Nature 45:416

Forbes HO (1892b) [*Diaphorapteryx* gen. nov.]. Bull Br Ornithol Club 4:xxi–xxii

Frohawk FW (1892) Description of a new species of rail from Laysan Island (North Pacific). Ann Mag Nat Hist 9:247–249

García-R JC, Matzke NJ (2021) Trait-dependent dispersal in rails (Aves: Rallidae): historical biogeography of a cosmopolitan bird clade. Mol Phylogenet Evol 159:107106

García-R JC, Gibb GC, Trewick SA (2014a) Deep global evolutionary radiation in birds: diversification and trait evolution in the cosmopolitan bird family Rallidae. Mol Phylogenet Evol 81:96–108

García-R JC, Gibb GC, Trewick SA (2014b) Eocene diversification of crown group rails (Aves: Gruiformes: Rallidae). PLoS One 9:e109635

Gill BJ, Bell BD, Chambers GK, Medway DG, Palma RL, Scofield RP, Tennyson AJD, Worthy TH (2010) Checklist of the birds of New Zealand, Norfolk and Macquarie Islands, and the Ross Dependency, Antarctica. 4th edition. Te Papa Press in association with OSNZ, Wellington

Gill F, Donsker D, Rasmussen P (2024) IOC World Bird List (v14.2). http://www.worldbirdnames.org/https://doi.org/10.14344/IOC.ML.14.2

Gmelin JF (1789) Caroli a Linné … Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 13th edition. Vol. 1, Part 2. 501–1032. Impensis Georg Emanuel Beer, Lipsiae [Leipzig]

Gould J (1837) Characters of some new species of birds from Swan River. Proc Zool Soc London 1836:85–86

Gould J (1843) Descriptions of thirty new species of birds from Australia. Proc Zool Soc London 1842:131–142

Gould J (1846) The birds of Australia. Volume 6. London

Gray GR (1855) Catalogue of the Genera and Subgenera of Birds Contained in the British Museum. Taylor & Francis, London

Gurney JH (1877) Additional notes on the ornithology of the Republic of Transvaal. By Thomas Ayres Ibis 1:339–354

Gussekloo SW, Cubo J (2013) Flightlessness affects cranial morphology in birds. Zoology 116:75–84

Hartlaub G, Finsch O (1871) On a collection of birds from Savai and Rarotonga Islands in the Pacific. Proc Zool Soc London 1871:21–32

Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: improving the ultrafast bootstrap approximation. Mol Biol Evol 35:518–522

Hodgson BH (1837) Indication of a new genus belonging to the Strigine family, with description of the new species and type. Madras J Literat Sci 5:23–25

Holdaway RN, Worthy TH (1997) A reappraisal of the late Quaternary fossil vertebrates of Pyramid Valley Swamp, North Canterbury, New Zealand. New Zealand J Zool 24:69–121

Horn PL (1983) Subfossil avian deposits from Poukawa, Hawke’s Bay, and the first record of *Oxyura australis* (Blue-billed Duck) from New Zealand. J R Soc New Zealand 13:67–78

Hume JP (2017) Extinct birds, 2nd edn. Bloomsbury, London

Hutton FW (1872) Notes on some birds from the Chatham Islands, collected by H. H. Travers, Esq.; with descriptions of two new species. Ibis 2:243–250

International Commission on Zoological Nomenclature (ICZN) (1985) International code of zoological nomenclature, 3rd edn. International Trust for Zoological Nomenclature, London

International Commission on Zoological Nomenclature (ICZN) (1999) International code of zoological nomenclature, 4th edn. International Trust for Zoological Nomenclature, London

Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. Nat Methods 14:587–589

Kirchman JJ (2009) Genetic tests of rapid parallel speciation of flightless birds from an extant volant ancestor. Biol J Linn Soc 96:601–616

Kirchman JJ (2012) Speciation of flightless rails on islands: a DNA-based phylogeny of the typical rails of the Pacific. Auk 129:56–69

Kirchman JJ, Rotzel McInerney N, Giarla TC, Olson SL, Slikas E, Fleischer RC (2021) Phylogeny based on ultra-conserved elements clarifies the evolution of rails and allies (Ralloidea) and is the basis for a revised classification. Ornithology 138:ukab042

Kittlitz FH (1858) Denkwürdigkeiten einer Reise nach dem russischen Amerika, nach Mikronesien und durch Kamtschatka 2. J. Perthes, Gotha

Kumar S, Stecher G, Tamura K (2016) MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. Mol Biol Evol 33:1870–1874

Kuročkin EN, Lopatin AV, Zelenkov NV (2015) Fossil vertebrates of Russia and adjacent countries – the reference book for paleontologists, biologists and geologists: fossil reptiles and birds, part 3. Russian Academy of Sciences Borissiak Paleontological Institute, Moscow

Leach WE (1816) Systematic catalogue of the specimens of the indigenous mammalia and birds that are preserved in the British Museum: with their localities and authorities. R. & A. Taylor, London

Leach WE (1820) Eleventh Room. In: Museum B (ed) Synopsis of the contents of the British Museum, seventeenth. British Museum, London, pp 65–70

Linnaeus C (1758) Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 10th edition. Laurentii Salvii, Holmiae [Stockholm]

Linnaeus C (1766) Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 12th edition. Part 1. Laurentii Salvii, Holmiae [Stockholm]

Livezey BC (1998) A phylogenetic analysis of the Gruiformes (Aves) based on morphological characters, with an emphasis on the rails (Rallidae). Philos Trans R Soc London B 353:2077–2151

Livezey BC (2003) Evolution of flightlessness in rails (Gruiformes: Rallidae): phylogenetic, ecomorphological and ontogenetic perspectives. Ornithol Monogr 53:1–654

Livezey BC, Zusi RL (2006) Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy: I. Methods and characters. Bull Carneg Mus Nat Hist 37:1–544

Lowe P (1923) Description of a new genus and species of rail, *Atlantisia rogersi*, from Inaccessible Island. Bull Br Ornithol Club 43:174–176

Lubbe P, Rawlence NJ, Dussex N, Kardialsky O, Knapp M (2025) Plio-Pleistocene environmental changes drove the settlement of Aotearoa New Zealand by Australian open-habitat bird lineages. Mol Ecol 34:e17648

Marchant S, Higgins P (1993) Handbook of Australian, New Zealand & Antarctic birds, vol 2. Oxford University Press, Melbourne

Mayr E (1933) Birds collected during the Whitney South Sea Expedition. XXII. Three new genera from Polynesia and Melanesia. Am Mus Novit 590:1–6

Mayr E (1986) The correct name of *Rallus hodgeni* [letter to the editor]. Notornis 33:268

Mayr G (2019) Hypotarsus morphology of the Ralloidea supports a clade comprising *Sarothrura* and *Mentocrex* to the exclusion of *Canirallus*. Acta Ornithol 54:51–58

Mayr E, Diamond J (2001) The birds of Northern Melanesia: speciation, ecology, and biogeography. Oxford University Press, United Kingdom

Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, Von Haeseler A, Lanfear R (2020) IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. Mol Biol Evol 37:1530–1534

Nitzsch CL (1820) Ueber die Nafendrüse der Vögel. Deutsch Arch Physiol 6:234–269

North AJ (1908) On three apparently undescribed birds from Henderson or Elizabeth Island, Paumotu Group. Rec Austr Mus 7:29–32

Oliver WRB (1955) New Zealand birds. 2nd ed. AH and AW Reed, Wellington

Olson SL (1973) Evolution of the rails of the South Atlantic Islands (Aves: Rallidae). Smithson Contr Zool 152:1–53

Olson SL (1974) A new species of *Nesotrochis* from Hispaniola, with notes on other fossil rails from the West Indies (Aves: Rallidae). Proc Biol Soc Wash 87:439–450

Olson SL (1975) A review of the extinct rails of the New Zealand region (Aves: Rallidae). Nat Mus New Zealand Rec 1:63–79

Olson SL (1976) Extinct rails [letter to the editor]. Notornis 23:79

Olson SL (1977) A synopsis of the fossil Rallidae. In: Dillon Ripley S (Ed) Rails of the World. A monograph of the family Rallidae. David R Godine, Boston, pp 339–373

Olson SL (1986) Emendation of the name of the fossil rail *Rallus hodgeni* Scarlett. Notornis 33:32

Olson SL (1987) More on the name *Rallus hodgenorum*. Notornis 34:167–168

Olson SL, James HF (1991) Descriptions of thirty-two new species of birds from the Hawaiian Islands: part I. Non-Passeriformes. Ornithol Monogr 45:1–88

Olson SL, Wingate DB (2000) Two new species of flightless rails (Aves: Rallidae) from the middle Pleistocene "crane fauna" of Bermuda. Proc Biol Soc Wash 113:356–368

Oswald JA, Terrill RS, Stucky BJ, LeFebvre MJ, Steadman DW, Guralnick RP, Allen JM (2021) Ancient DNA from the extinct Haitian Cave-rail (*Nesotrochis steganinos*) suggests a biogeographic connection between the Caribbean and Old World. Biol Lett 17:20200760

Owen R (1848) On the remains of the gigantic and presumed extinct wingless or terrestrial birds of New Zealand (Dinornis and Palapteryx), with indications of two other genera (Notornis and Nestor). In: Proceedings of the Zoological Society of London XVI, pp 1–11

Reichenbach HGL (1853) Avium Systema Naturale. i–viii, 1–36, i–xxxi. Friedrich Hofmeister, Leipzig

Ridgway R (1920) Diagnoses of some new genera of birds. Smithson Misc Coll 72:1–4

Rothschild W (1903) *Hypotaenidia wakensis* n. sp. Bull Br Ornithol Club 13:75

Sangster G, García-R JC, Trewick SA (2015) A new genus for the Lesser Moorhen *Gallinula angulata* Sundevall, 1850 (Aves, Rallidae). Eur J Taxon 153:1–8

Scarlett RJ (1955) A new rail from South Island swamps in New Zealand. Rec Canterb Mus 6:265–266

Scarlett RJ (1969) Moas and other birds. In: Knox GA (Ed) The natural history of Canterbury. A.H. & A.W. Reed, Wellington, pp 565–568

Scarlett RJ (1970a) A small woodhen from New Zealand. Notornis 17:68–74

Scarlett RJ (1970b) The genus *Capellirallus*. Notornis 17:303–319

Scarlett RJ (1976) Extinct rails [letter to the editor]. Notornis 23:78

Slikas B, Olson SL, Fleischer RC (2002) Rapid, independent evolution of flightlessness in four species of Pacific island rails (Rallidae): an analysis based on mitochondrial DNA sequence data. J Avian Biol 33:5–14

Sparrman A (1786) Museum Carlsonianum, in quo novas et selectas aves, coloribus ad vivum brevique descriptione illustratas, suasu et sumtibus generosissimi possessoris. Ex Typographica Regia, Holminae

Steadman DW (1986) Two new species of rails (Aves: Rallidae) from Mangaia, southern Cook Islands. Pac Sci 40:27–43

Steadman DW (2006) Extinction and biogeography of tropical Pacific birds. University of Chicago Press, Chicago & London

Stervander M, Ryan PG, Melo M, Hansson B (2019) The origin of the world's smallest flightless bird, the Inaccessible Island Rail *Atlantisia rogersi* (Aves: Rallidae). Mol Phylogenet Evol 130:92–98

Storer RW (1971) Adaptive radiation of birds. In: Farner DS, King JR, Parkes KC (eds) Avian biology, vol I. Academic Press, New York and London, pp 149–188

Sundevall CJ (1850) Om Wahlbergs foglar från Södra Afrika. Öfv Kongl Vetensk-Akad Förhandl 7:96–111

Swainson W (1829) Zoological illustrations, or, original figures and descriptions of new, rare, or interesting animals, selected chiefly from the classes of ornithology, entomology, and conchology, and arranges according to their apparent affinities. Volume 1, Second series. Baldwin and Cradock, London

Taylor PB (1998) Rails: a guide to the rails, crakes, gallinules and coots of the world. Yale University Press, New Haven, Connecticut

Uyehara K (2004) First record of Sora in the State of Hawaii. West Birds 35:47–49

van Beneden P-J (1876) A new fossil bird, *Anas finschi*, from the Earnscleugh Caves, Otago, New Zealand. Ann Soc Géol Belg 2:599–602

van Tets G (1984) A checklist of extinct fossil Australasian birds. In: Archer M, Clayton G (eds) Vertebrate zoogeography & evolution in Australasia (animals in space & time). Hesperian Press, Perth, pp 469–475

Vieillot LP (1816) Analyse d'une Nouvelle Ornithologie Élémentiare. Deterville, Paris

Vieillot LP (1819) Rale a face noire, *Rallus melanops* In: Par une Société de Naturalistes et d'Agriculteurs (ed) Nouveau Dictionnaire d'Histoire Naturelle, vol. 28. Deterville, Paris, p 553

Worthy TH (1997) The Quaternary fossil fauna of South Canterbury, South Island, New Zealand. J R Soc New Zealand 27:67–162

Worthy TH (1998) Quaternary fossil faunas of Otago, South Island, New Zealand. J R Soc New Zealand 28:421–521

Worthy TH, Holdaway RN (1996) Quaternary fossil faunas, overlapping taphonomies, and palaeofaunal reconstruction in North Canterbury, South Island, New Zealand. J R Soc New Zealand 26:275–361

Worthy TH, Holdaway RN (2000) Terrestrial fossil vertebrate faunas from inland Hawke's Bay, North Island, New Zealand. Part 1. Rec Canterbury Mus 14:89–154

Worthy TH, Holdaway RN (2002) Lost world of the moa. Indiana Univ. Press, Bloomington

Worthy TH, Mildenhall DC (1989) A late Otiran-Holocene paleoenvironment reconstruction based on cave excavations in northwest Nelson, New Zealand. New Zealand J Geol Geophys 32:243–253

Worthy TH, Nguyen JM (2020) An annotated checklist of the fossil birds of Australia. Trans R Soc S Austr 144:66–108

Worthy TH, McInerney PL, Blokland JC (2025) The Late Pleistocene and Holocene of Oceania. Encyclopedia of Quaternary Science (Third Edition) 6:521–540

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